

On the Second Abdominal Segment in a Few Libellulidæ.

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In the spring of 1892, I made, in connection with my work in the zoölogical department in Wellesley College, a somewhat careful study of the second abdominal segment and the penis in a few male Libellulinae. Though I was unable to do all that I had planned, it seems worth while to publish my results in spite of their fragmentariness, since they may serve as a basis for the work of some one else.

I wished to learn the details of external structure in this part of the body and to determine as far as possible the homologies of the various parts. The species studied were *Diplax rubicundula* and *vicina*; *Celithemis elisa*; *Libellula pulchella*, *quadrupla* and *exusta*; *Plathemis trimaenulata*. I will begin by a full description of *Diplax rubicundula*, and then follow this by a brief statement of the more important respects in which the other species studied differ from this one.

The second abdominal segment, like most of the others, consists of a narrow ventral piece, and a broad dorsal piece covering both back and sides of abdomen. The first is the sternum; the second, the tergum. The tergum (Fig. 1) is made up of three sclerites which form a longitudinal series. The suture between the first and the second is present only on the dorsal half of the segment, becoming obsolete as it approaches the sides; that between the second and third is distinct for its entire extent. Each side of the second sclerite is produced caudolaterally into a rounded process called the genital lobe (*a*). The third sclerite is shorter than either of the others; it ends abruptly at the base of genital lobe. The sternum (*e*, Fig. 2) consists of but one sclerite. This is nearly as long as the first tergal one and lies ventrad of it, the cephalic edge a little caudad of the cephalic edge of the tergum. The cephalo-lateral angles are produced into wing-like processes (*f*) which underlie the tergum and serve for the attachment of muscles. Caudad of the sternum is a long extent of membrane which lies ventrad of the caudal part of the tergum, and where it meets the sternum is so infolded as to make a recess over which the latter projects like a pent-house roof. Indeed, except at its very cephalic edge, the whole sternum bulges out to a greater or less degree from the rest of the segment.

On the membranous surface directly caudad of the sternum lie a pair of stout appendages (*g*) called hamules, readily to be seen with the naked eyes. Each is a thick, laterally compressed and somewhat elongated organ which is cleft distally into two divisions; a short, strong spur ending in an incurved, strongly chitinized tip (*h*), and a truncate shorter portion (*i*) having the face turned towards the spur concave. The hamule projects ventrad and the lobes lie cephalad and caudad; the

truncate lobe is the more caudal. The divisions vary greatly in length and shape in different species, though they generally form, as in *Diplax rubicundula*, about one-third of the length of the entire appendage. From the point of bifurcation, a ridge extends for a considerable distance towards the base of the hamule. The mesal face of the organ is largely membranous, especially at the base, so that the hamule can be flexed freely towards its fellow of the opposite side.

The hamules are borne by a chitinous framework (*k*), in shape roughly resembling a U, and attached by its tips to the inner face of the ventral sclerite. It seems to arise as a local chitinization of the membrane which lies caudad of this sclerite. Projecting from either side of the framework just caudad of the sclerite is a short rod (*m*) to which is attached one of the hamules. On the median part of the framework is borne a triangle (Fig. 3, *n*). Its apex end is cephalad; its cephalo-lateral sides are chitinized, though elsewhere it is membranous; and its base projects more or less caudad of the framework. The basal angle of either side forms a second, posterior point of attachment for the hamule of that side.

Another conspicuous structure is attached just caudad of the framework on the median line (Fig. 2). When extended as in the diagram, its tip points cephalad, but the distal end is ordinarily flexed upon the proximal part. The organ consists of an enlarged basal portion, the genital bladder, and of a slender, rodlike distal part, the penis. The genital bladder is a somewhat hemispherical body. The caudal half of its dorsal surface is attached for nearly its entire width to the underlying part of the abdomen and the rest of the dorsal face is chitinized. The ventral face is imperfectly chitinized, the chitin being deposited in three triangles; a median caudal one (*r*) and two cephalo-lateral ones (*o* and *r*), all separated from one another by band-like membranous interspaces, which, evidently, afford opportunity for variations in the size of the bladder. This mode of attachment of the bladder causes the structure of which it constitutes the base to appear as an appendage of the second segment; it does really, however, belong to the third, as is clearly seen in *Celithemis elisa*.

The penis consists of three segments; the first two are very simple, but the third is extremely complicated. The first is chitinized continuously on its dorsal surface, but the second, though in the main chitinous on this aspect, is membranous on the dorso-mesal line. Both are membranous ventrally and this condition is evidently correlated with the fact that in the position of rest this portion is covered by the reflexed tip of the penis. What we have called the third segment consists of two entirely distinct sclerites and of a cluster of appendages, some membranous and some chitinous, borne at the extreme tip of the organ. The larger and more proximal sclerite (1) constitutes the dorsal aspect of the segment. It is somewhat shield-shaped, but the distal angles are prolonged and curved around to the ventral side where they almost meet.

For convenience we shall term it the shield. When the penis is flexed, the distal part is protected by the overlying hamules so that this sclerite is the only portion exposed. The point of flexion is just proximal of it, which accounts for its very limited extent on the ventral aspect. The second sclerite (2) is narrower than the first, is irregularly ring-shaped and lies just distad of the shield. We shall call this the ring. As will be seen later, it encircles most but not all the divisions of the penis-tip. Distad of the ring on the dorso-mesal line is a chitinized body (5), which divides into slender, tapering horns; it is recognizable by its honey-yellow color and we shall call it the fork. Arising from nearly the same place are two membranous lobes (4), with transverse rows of closely set chitinous hairs. These may be contracted into roundish masses which, because of the brown hair, seem on first appearance to be chitinized. When extended, as in the plate, they appear bannerlike, and we shall term them the banners. Near the base of each is a small cluster of long, stout bristles. Laterad of the banners are two blunt lobes (6), somewhat membranous proximally but strongly chitinized toward their distal end. As these are in many species somewhat twisted, we have termed them the twists. Pressure on the genital bladder causes them to rotate laterad and ventrad; they may possibly serve, therefore, to retain the hold of the penis-tip within the vulva. Ventrad of all the others lies a large, membranous lobe which somewhat resembles the shape of a monk's hood and which we have called the hood (3). With a view to possible homologies it is well to note the relative position of these structures. The penis viewed from the tip presents a depression or pit guarded above by the fork, below by the hood, laterad by the banners and these again are guarded laterad by the twists. The ring lies entirely dorsad of the hood and does not encircle it. According to Rathke, there is in *L. aenea* a minute opening at the penis-tip.

In *Diplax vicina*, the ventral sclerite is deeply emarginate, and its caudo-lateral angles are strongly chitinized. The hamules are small and inconspicuous (Fig. 5, *g*). The basal portion is short and the two lobes are of about equal length. The tip of the anterior lobe is strongly chitinized and very markedly incurved.

The last division of the penis consists of but one sclerite in addition to the cluster of appendages at the tip. This sclerite is long on the dorsal and short on the ventral aspect, where its edges nearly but not quite meet. Its general shape would seem to indicate that it is formed by the fusion of the shield and ring; moreover it bears a pair of short transverse ridges which look like the indications of such fusion. But as the sclerite encloses the hood as well as the other part of the penis-tip, it seems probable that no part of it corresponds to the ring, but that this sclerite is entirely wanting in the present specimen. The penis-tip is divided into a dorsal and a ventral portion. The ventral part is a rounded lobe, thickly beset with hairs; the dorsal part forms a membranous base from which arise three pairs of appendages. Beginning

at the most proximal, these appendages are a pair of horns, twisted at the base; a pair of membranous lobes, thickly beset with hairs irregularly arranged; and lastly two slender horns (Fig. 6).

We appear to have in *Diplax vicina* a more primitive condition than in *Diplax rubicundula*, in that the base which bears the appendages at the penis-tip is elongated so that they arise in succession instead of forming a clump. The inner horns are very probably the result of the division of the fork of *D. rubicundula*, and the other parts appear to be homologous respectively with the hood, the twists and the banners of that insect.

In *Celithemis elisa*, the mesal part only of the caudal edge of the ventral sclerite is emarginate. The hamules are inconspicuous, being but little larger than the genital lobes; their basal part is membranous or but slightly chitinized and the lobes are long, stout, and of nearly equal length. The framework which bears the hamules is strongly chitinized; its lateral projections (Fig. 8, *m*) are long and stout; the part of the median triangle (*n*) cephalad of the framework is short, but the triangle extends caudad farther than in other forms.

In the genital bladder the two latero-cephalic triangles of the ventral face are replaced by a single sclerite, somewhat cleft mesally, which apparently corresponds to the two united. The bladder is attached only by a small proximal neck and the dorsal aspect bears a tapering triangular sclerite (Fig. 9, *s*), each basal angle of which is attached to one side of the sclerite (*v*).

As to the distal segment of the penis, the shield is a broad sclerite, bearing lateral hornlike projections which point ventrad. The ring is of smaller diameter, but is very long, and has in general much the shape of a boddice; its edges meet on the dorsal line, but, so far as I can make out, do not unite. These edges are prolonged distad into two rodlike pieces (2). The fork is represented by a thick yellow sclerite, somewhat bifid, which lies close beneath but is quite free from these pieces (5). Laterad and proximad of the fork are a pair of tiny membranous lobes apparently corresponding to the banners (4). The hood is a large membranous lobe, thickly beset with hairs (3).

In this species, the twists of *D. rubicundula* appear to be entirely wanting. It is just possible, of course, that they may have moved dorsad and fused with the ring forming the rodlike projections of the sclerite. I have, however, no evidence tending to show that this has taken place, and in the absence of such evidence it cannot be assumed. We must suppose, therefore, that the twists are absent and that these rodlike projections are new developments. The advantage of having the genital bladder provided with three sclerites seems evident, so that *C. elisa* is probably primitive, since retrogression is hardly likely to be accomplished by fusion. There seems some slight reason for believing also that the condition of the fork found in this species is the original one, and that the two horns found in *D. vicina* have arisen by the division of

what was originally a single sclerite, while the condition in *D. rubicundula* represents an intermediate stage.

The relation of the parts in these three species are, in the main, tolerably clear. But when we turn to *Libellula* the problem is much more complicated. Not only have I not been able to homologize the parts found in *Diplax* and those of this genus, but I have also found it impossible to determine the relations of the parts found in different species of *Libellula*. I can therefore give little more than a bare description.

We may begin with *Libellula exusta*. The general arrangement is much as in *Diplax*. The genital lobes are short and stout. The ventral sclerite is wide, short, and only slightly emarginate caudally (Fig. 11, *e*). The lateral parts of the free edges are somewhat undulate. The hamules are stout and are membranous proximally, and the tip of the spur is very strongly incurved. The framework is wide and strong. The lateral rods are connected for their entire length to that part of the framework caudad of them by feebly chitinized triangles (*x*). The triangle (*u*) borne by the middle part of the framework is very long; its apex lies under the free edge of the ventral sclerite.

The cephalic part of the bladder is chitinized in a single sclerite with a mesal cleft. The last segment of the penis is made up mainly of a single large sclerite (Fig. 12, *p*₃), much longer on the dorsal than on the ventral surface. Its edges approach but do not quite meet on the ventrimeson. There is a curious dorsal hump on the distal part of the sclerite and the distal edge bears ventrally a pair of small, spine-like projections. If this sclerite is the result of the fusion of the shield and the ring there is no indication of the fact. As to the distal part of the segment, it projects only slightly beyond this sclerite; it consists of two pairs of appendages rising from a full membranous base. The median and dorsal pair are sigmoid rods curved towards the dorsal surface at their distal ends (*u*). The second pair are membranous at base but strongly chitinized distally (*v*).

I would suggest the following as the possible homologies of some of these parts: the large sclerite corresponds to the shield; the ring is wanting; the hood is represented in a much less differentiated state than in *Diplax*, by the full membranous portion of the penis-tip. As to the homologies of the other parts I am entirely uncertain.

In *Libellula pulchella*, the blunt division of the hamule lies almost laterad instead of caudad of the spur; it is moreover reduced nearly to a knob. The spur is long and strong and its point turns laterad.

The dorsal aspect of the genital bladder, though normally united for a considerable portion of its extent with the abdomen, separates readily therefrom after maceration in caustic potash. In the penis, the first segment is extremely long and bears a dorsal terminal tubercle; the second segment is very small and triangular; the third bears distally a large dorsal upgrowth. The edges of this sclerite do not quite meet ventrally, and between the angles projects a small membranous lobe which per-

haps corresponds to the hood of *Diplax*. Attached to the base of this structure on either side is a tiny, membranous, finger-like lobe. The tip of the penis is formed by a great mass of membrane which projects from the distal end of the third sclerite described above. This membrane is covered with scattered chitinized papillae and is chitinized in such a way as to form a pair of irregularly shaped sclerites, somewhat like a moose's antlers, narrow at the base, broadening distally and uniting dorsally and ventrally so as to form a ring which divides the membrane into a proximal and a distal division. This arrangement will be made clear by a glance at the diagram (Fig. 14). At the base of these sclerites on either side is a small piece visible after the removal of the shield; these pieces appear to be rudiments of structures much more developed in *L. quadrupla*.

In *L. quadrupla*, the general appearance is much the same as in the species last described; there are, however, one or two interesting differences in the penis-tip. The hood is bi-lobed and so far as I could discover, there are no such lobes laterad of it as in *L. pulchella*. The membranous tip of the penis is not chitinized in any part, but the chitinous papillae with which it is beset are much more closely placed in a region which corresponds with that part which in *L. pulchella* is chitinized. It seems possible that this massing of papillae is, so to speak, an attempted adaptation to certain unknown conditions and that the chitinization is a more satisfactory adaptation to the same conditions. The dorsi-mesal portion of the membrane is largely free from papillae and is extended into a long, finger-like, membranous tip.

Platthemis trimaculata is in several respects a most interesting species. The first abdominal segment bears on its ventral aspect a pair of chitinous lobes; these structures have a position on the first segment exactly corresponding to that which the hamules occupy on the second, and their form is not unlike that of the undivided hamules found in many kinds of Libellulinae. They are, however, continuous with the abdominal wall instead of being jointed to it as are the hamules.

In the second segment, the sternum is short; it bears on its free edge a small median lobe which is indented on the mesal line so as to form two scallops (Fig. 16). The hamules show only very slight differentiation into lobes. The cephalic lobe, which corresponds to the spur of the ordinary hamule, is shaped somewhat like a man's boot, the toe of the boot being turned towards the caudal lobe. The toe alone is free, but from the point of division between the two lobes a membranous band extends towards the base of the hamule; if this membrane were unfolded the condition found in the other Libellulinae would be produced. The caudal lobe is deeply grooved at its tip so that it appears almost bi-lobed. I am unable to describe the penis.

This species seems to me to give us some reason to believe that the hamules are the survivors of the series of abdominal appendages present in the ancestor of the insects. And in this connection, I would suggest

the possibility that the penis is to be regarded as the fused and greatly modified abdominal appendages of the third abdominal segment. The hamules of *Plathemis* also afford us a suggestion of the way in which the branched may have arisen from the simple condition.

Conclusion: While my work has been mainly description, there are a few general suggestions which may be thrown together here. 1. There seems some reason for believing that the hamules are homologues of abdominal appendages. 2. Various stages are observed between the ordinary bifid condition of the hamules and the uniramous condition of other subfamilies. As we have no reason to believe that the abdominal appendages were originally biramous, we must suppose the condition in *Libellulinae* a secondary one. 3. It has been impossible to homologize the appendages of the penis-tip, though there seems some reason to think that wider study might enable one to do it. 4. The resemblance between these appendages in *Diplax vicina* and *rubicundula* is very close; *Celithemis elisa* is quite different in some respects. This species was formerly placed in the genus *Diplax*; the marked difference and the general similarity of the penis-tip is what we should expect in two genera so closely related as to have been formerly classed as one and leads us to believe that the study of this organ may prove to be of systematic importance. In conclusion, I wish to acknowledge the valuable aid given me by Prof. M. A. Willcox in the preparation of this paper, both in general suggestion and revision. I have found no literature which was of value save Rathke's paper, "De Libellarum Partibus Genitalibus."

DESCRIPTION OF DIAGRAMS, PLATES XIV AND XV.*

Diplax rubicundula.

- Fig. 1. One-half of tergum.
- Fig. 2. Second segment—ventral view.
- Fig. 3. Framework, triangle, and hamules.

Diplax vicina.

- Fig. 4. Second segment—ventral view.
- Fig. 5. Framework, triangle, hamules, and sternum.
- Fig. 6. Genital bladder and side-view of penis.

Celithemis elisa.

- Fig. 7. Second segment—ventral view.
- Fig. 8. Framework, triangle, hamules, and sternum.
- Fig. 9. Genital bladder and penis—dorsal view.

Libellula exusta.

- Fig. 10. Second segment—ventral view.
- Fig. 11. Framework, triangle, hamules, and sternum.
- Fig. 12. Genital bladder and side-view of penis.

*The scale by which drawings were made differs, but as size in mm. is given, there need be no misunderstanding.

Libellula pulchella.

Fig. 13. Framework, triangle, hamules, and sternum.

Fig. 14. Genital bladder and side view of penis.

Libellula quadrupla.

Fig. 15. Genital bladder and penis—side view.

Plathemis trimaculata.

Fig. 16. Framework, triangle, hamules, and sternum

Fig. 17. Genital bladder and penis—ventral view

Fig. 18. Penis—dorsal view.

In the above diagrams, the letters stand for organs as follows :

a. Genital lobe. *b.* First segment of tergum. *c.* Second segment of tergum. *d.* Third segment of tergum. *e.* Sternum. *f.* Triangular appendage of sternum. *g.* Hamule. *h.* Spur of hamule. *i.* Truncate lobe of hamule. *k.* Framework. *m.* Lateral rod of framework. *n.* Triangle. *o.* Left cephalic triangle of genital bladder. *p₁, p₂, p₃.* Segments of penis. *r.* Right cephalic triangle of genital bladder. *s.* Dorsal triangle in genital bladder of *Celithemis elisa*. *t* and *y.* appendages of penis of *Plathemis trimaculata*. *u* and *v.* Appendages of penis of *Libellula exusta*. *w.* Caudal triangle of genital bladder. *x.* Membranous appendage of framework in *Libellula exusta*. 1. Shield of third segment of penis. 2. Ring. 3. Hood. 4. Banner. 5. Fork. 6. Twist.